Marivaux et al.

Anthropoid primates from the Oligocene of Pakistan (Bugti Hills): Data on early anthropoid evolution and biogeography

Supporting Information

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Supporting Text

Description of Fossils

Systematic Palaeontology

(*Figures cited in this section are those of the article*)

Order Primates Linnaeus, 1758; Suborder Anthropoidea Mirvart, 1864; Family Amphipithecidae Godinot, 1994

Included Genera. Pondaungia Pilgrim, 1927; "*Amphipithecus*" Colbert, 1937; *Siamopithecus* Chaimanee *et al.*, 1997; *Myanmarpithecus* Takai *et al.*, 2001; *Bugtipithecus* gen. nov. "*Amphipithecus*" is also considered by some authors (1) as a junior synonym of *Pondaungia*.

Bugtipithecus inexpectans Sp. Nov.

Holotype. UMC-DBC 2174, right M^1 (Fig. 2*J*), temporarily housed in the Palaeontology Department, University of Montpellier, France.

Hypodigm. UMC-DBC 2172, left M^1; UMC-DBC 2173, left M^2; UMC-DBC 2191, left P^4; UMC-DBC 2178, left P_4; UMC-DBC 2177, right M_1; UMC-DBC 2175, right M_3; UMC-DBC 2176, left M_3.

Description. The left P^4 (UMC-DBC 2191; Fig. 2 *N* and *O*; Table 1) attributed to *Bugtipithecus* is suboval and exhibits a simple bicuspidate morphology. The paracone is the largest cusp, which is high, conical, and situated near the buccal margin of the crown. Distal to the paracone, a small swelling of enamel may correspond to a small metastyle. The parastyle is in contrast minute to indistinct. The protocone is well inferior to the paracone and its lingual wall forms the lingual margin of the crown. The postprotocrista is strong, and it terminates on the postcingulum. The preprotocrista is short and transverse, and it joins a tiny hypoparacrista. Cingula occur only on the mesial and distal margins of the tooth.

The two upper molars identified here as right M^1 (UMC-DBC 2174, the Holotype; Fig. 2 *J* and *M*) and left M^2 (UMC-DBC 2173; Fig. 2*K*) bear quite similar dental morphology. The

posterior margin of M^1 is slightly more waisted than that of M^2 and differs mainly in showing a greater development of its parastyle and metastyle. Both teeth are characterized by salient and equally sized protocone, paracone and metacone, and by the presence of well-marked and continuous anterior, posterior, buccal and lingual cingula, surrounding the teeth. The anterocingulum is uninterrupted on the mesial side of the tooth, running continuously from the protocone to the parastyle. The lingual cingulum is strong and complete, and it bears a large cuspidate hypocone, situated slightly distolingually with respect to the protocone. A strong prehypocrista connects the hypocone with the postprotocrista. The postprotocrista runs distobuccally and ends against the lingual face of a minute metaconule. A tiny, short hypometacrista occurs between the metacone and the metaconule. The preprotocrista runs mesiobuccally, eventually joining a strong hypoparacrista. The hypometacrista and hypoparacrista are parallel and mesiolingually oriented (oblique). A minute swelling, occupying the position of a paraconule, can be observed on M^2, which is indistinct on M^1. The trigon basin is relatively shallow and closed buccally by the presence of a moderately elevated centrocrista.

Among the lower teeth, we have identified one left P_4 (UMC-DBC 2178), one right M_1 (UMC-DBC 2177), and two M_3 (right UMC-DBC 2175, and left UMC-DBC 2176). The P_4 (Fig. 2 *C*, *F*, *I*, *L*) is characterized by an inflated protoconid, which represents the main cuspid of the tooth. The paracristid is weakly developed and shows a small swelling in its lingual extremity. The specimen bears a distinct metaconid, which is located distally with respect to the protoconid and much lower on the crown. The premetacristid is not developed and the trigonid is lingually open. The talonid is lower and mesiodistally shorter than the trigonid. Distal to the protoconid, the hypoconid is the only distinct talonid cuspid. The talonid is lingually and distally bordered by a low hypocristid, which is connected to the weakly elevated and short postmetacristid. The cristid obliqua is lacking and the talonid remains open buccally. The buccal cingulid is only developed between the hypoconid and the protoconid.

The three molars are characterized by wide talonid basins and massive development of their lingual talonid walls, which are marked by deep notches that separate the postmetacristid from the pre-entocristid. On M_1 (UMC-DBC 2177; Fig. 2 *B*, *E*, *H*), the metaconid lies slightly distolingual to the protoconid and is extended distally and mesially by the development of a strong and elevated postmetacristid and a short premetacristid, respectively. The trigonid of M_1 is slightly higher than the talonid, buccolingually pinched, mesiodistally enlarged, and lingually closed. The low paracristid shows a minute swelling reminiscent of a paraconid. The main cuspids of the trigonid are moderately inflated and the entoconid is slightly distal to the

hypoconid. The postentocristid is strong and elevated, and connects the hypocristid slightly buccally to midline. There is no hypoconulid. The buccal cingulid is limited between the protoconid and the hypoconid. The cristid obliqua is round and weakly elevated, and reaches the base of the trigonid wall at a point distal to the protoconid. The hypoflexid is shallow.

The two M_3 (UMC-DBC 2175 and UMC-DBC 2176; Fig. 2 *A*, *D*, *G*) referred to *Bugtipithecus* display a dental pattern that is similar to that of M_1 but differ in showing greater development of the premetacristid, a postmetacristid that is more lingually directed, an indistinct entoconid on the strong lingual talonid marginal crest, and in having a narrow talonid heel that is lingual in position. Both the protoconid and the hypoconid occupy a marginal buccal position. The cristid obliqua is nearly lateral and reaches the base of the trigonid wall.

Family Eosimiidae Beard *et al.*, 1994

Included genera. *Eosimias* Beard *et al.*, 1994; *Bahinia* Jaeger *et al.*, 1999; *Phenacopithecus* Beard and Wang, 2004; *Phileosimias Gen. Nov*.

Phileosimias kamali Sp. Nov.

Holotype. UMC-DBC 2199, right M^1 (Fig. 3*F*), temporarily housed in the Palaeontology Department, University of Montpellier, France.

Hypodigm. UMC-DBC 2192, left M^1; UMC-DBC 2196, left M^1; UMC-DBC 2194, left M^2; UMC-DBC 2197, left M^2; UMC-DBC 2200, left M^2; UMC-DBC 2193, right M^2; UMC-DBC 2202, right M^2; UMC-DBC 2198, left M^3; UMC-DBC 2195, right M^3; UMC-DBC 2201 right M^3; UMC-DBC 2203, right P_3; UMC-DBC 2204, left P_4; UMC-DBC 2205, left P_4; UMC-DBC 2206, left M_1; UMC-DBC 2209, left M_1; UMC-DBC 2211, left M_1; UMC-DBC 2207, left M_2; UMC-DBC 2210, left M_2; UMC-DBC 2212, left M_2; UMC-DBC 2213, left M_2; UMC-DBC 2214, left M_2; UMC-DBC 2215, left M_3; UMC-DBC 2216, left M_3; UMC-DBC 2217, left M_3; UMC-DBC 2208, right M_3; UMC-DBC 2218, right M_3; UMC-DBC 2219, right M_3.

Description. Among the isolated upper teeth attributed to *Phileosimias kamali*, only molars have been recovered. M^1 (Fig. 3 *A* and *F*) and M^2 (Fig. 3 *B* and *G*) differ in size ($M^2 > M^1$; Table 1) and shape (M^1 triangular, M^2 more quadrangular) but have a similar pattern of cusp and crest arrangement. Both teeth are characterized by bulbous and equally sized protocone (lingually inflated), paracone and metacone, moderately developed paraconule and metaconule, and considerable expansion of the stylar regions. The metacone and paracone are mesiodistally aligned, but the metacone show a slight buccal expansion. Both cusps have short, low, and mesiodistally oriented premetacrista and postparacrista, respectively. A strong and curved postmetacrista links the metacone and the metastyle, which is located buccal to the metacone. The parastyle is mesial to the paracone, being connected to it by a short preparacrista. The buccal cingulum is broad and extends from the parastyle to the metastyle. The protocone is linked to the metaconule and the paraconule by strong post- and preprotocristae, respectively (U-shaped protocone). The paraconule is smaller than the metaconule and connected to the parastyle by a thin and elevated preparaconule crista. There is no postmetaconule crista, hypoparacrista and hypometacrista, and the conules are separated from the metacone and the paracone by narrow and shallow grooves. The postcingulum is complete and broad, and shows (especially on M^1) a minute swelling of enamel in its distolingual part. The anterocingulum is strong but short (limited to its lingual part). The lingual cingulum is indistinct to absent and the lingual wall of the protocone, nearly vertical, forms the lingual margin of the crown.

The dental organization of M^3 (Fig. 3 *C* and *H*) is similar to that of M^{1-2} but differs in having a smaller metacone distal to the paracone, the postcingulum restricted to the lingual part of the crown, a minute metaconule, and in lacking the metastyle.

The composite lower dentition attributed to *Phileosimias kamali* includes P_3, P_4, M_1, M_2 and M_3. UMC-DBC 2203 is a right P_3 (Fig. 3 *X* and *Y*) characterized by a relatively simple crown morphology without paraconid, metaconid nor entoconid, but showing a high and conical protoconid. The talonid is mesiodistally shorter than the trigonid and displays a small swelling of enamel distal to the protoconid that corresponds to a minuscule hypoconid. A tiny and rounded hypocristid forms the distal talonid crest that reaches the lingual margin of the tooth. The hypoconid and the protoconid are linked by a thin and mesiodistally oriented cristid obliqua, which runs up the distal slope of the protoconid. The tooth is damaged at the base of the crown, rendering it difficult to determinate whether a cingulid occurs on the entirely periphery of the crown.

The P_4 of *Phileosimias kamali* is documented by two specimens (UMC-DBC 2204, UMC-DBC 2205), one of which is well-preserved and described here (UMC-DBC 2204; Fig. 3 *K*, *O*, *S*, *W*). Like P_3, P_4 has two roots that are aligned but slightly oblique with respect to the mesiodistal axis of the tooth, and its crown is moderately exodaenodont and morphologically more complex than that of P_3. The trigonid, which is dominated by the protoconid, is slightly longer than the talonid. The metaconid is situated inferiorly and distolingually with respect to the protoconid. The postprotocristid is complete but thin and low, and joins the protoconid with the metaconid. There is a small swelling of enamel at the mesiolingual extremity of the paracristid that could correspond to a very small paraconid. This small swelling is mesial to the metaconid and widely spaced from it. The postmetacristid is strong and elevated, and runs distally to merge with the short hypocristid. There is no entoconid. The hypoconid appears as a tiny cuspid, distal to the protoconid. The cristid obliqua is low and lateral, and joins the hypoconid with the protoconid. The buccal cingulid is complete and runs from the hypoconid to the paraconid at the base of the crown. In contrast, there is no trace of a lingual cingulid.

M_1 and M_2 share a similar pattern of crown morphology but differ in some details noted on the trigonid. Both teeth exhibit a paraconid distinctly cuspidate but nonetheless lower than the protoconid, which is slightly lower than the metaconid. On M_1 (Fig. 3 *L*, *P*, *T*), the paraconid is nearly mesial to the metaconid and widely spaced from it. On M_2 (Fig. 3 *M*, *Q*, *U*), the trigonid is mesiodistally pinched and therefore less open than on M_1, and the paraconid occurs between the protoconid and the metaconid. The trigonid is distinctly higher than the talonid, and its distal wall (postprotocristid) is deeply notched. On M_1, the trigonid is buccolingually narrower than the talonid, whereas on M_2, trigonid and talonid are similar in width. The hypoconid and the entoconid are equally sized and transversely aligned. A cuspidate but mesiodistally pinched hypoconulid occurs distally and slightly lingual to midline in position. Distolingually, a small sulcus separates the hypoconulid from the entoconid. Moderately developed postmetacristid and pre-entocristid form the lingual wall of the talonid. Both crests generally do not merge together and generate a narrow notch. Buccally, the hypoflexid is shallow, and a trenchant cristid obliqua runs from the hypoconid to the base of the trigonid wall at a point distal to the protoconid. The buccal cingulid at the crown base is well-developed and mesiodistally continuous between the paraconid and the hypoconulid.

Except for the presence of a stronger hypoconulid, which forms a heel on the talonid, the M_3 (Fig. 3 *N*, *R*, *V*) displays a dental configuration very similar to that of M_2 (Fig. 3*Q*). Comparatively, the tooth is longer and narrower than M_2, the buccal cingulid is less apparent

at the level of the hypoconid, and the postmetacristid is less developed. However, the latter character varies across the sample of M_3 recovered.

Phileosimias brahuiorum Sp. Nov.

Holotype. UMC-DBC 2221, right M^2 (Fig. 3*I*), temporarily housed in the Palaeontology Department, University of Montpellier, France.

Hypodigm. UMC-DBC 2220, right M^3; UMC-DBC 2222, right $M^{1/2}$.

Description. UMC-DBC 2221 (Fig. 4 *D* and *I*) is a right M^2 showing a perfect rectangular outline (with the long axis being buccolingual; Table 1), and highly cuspate protocone, metacone, and paracone. The paraconule and the metaconule are moderately developed and equivalent in size, and both are connected to the protocone by the preprotocrista and the postprotocrista, respectively (U-shaped protocone). There is no junction between the conules and the buccal cusps. The preparaconule crista is very thin and joins the anterocingulum. The buccal cingulum is broad and continuous between the metastyle and the parastyle, which are both crestiform. The lingual cingulum is complete, joining the anterocingulum with the postcingulum. Distally, the lingual cingulum displays a small swelling of enamel that corresponds to a minute hypocone.

UMC-DBC 2220 (Fig. 4 *E* and *J*) is a right M^3 showing the same morphological characteristics that occur on $M^{1/2}$ with conules that are equivalent in size, a thin preparaconule crista, and complete lingual and buccal cingula. This tooth is characterized by a reduced metacone, which is located slightly lingual to the paracone. The posprotocrista is directed toward the metaconule but does not reach it. In contrast, the metaconule is connected to the postcingulum. The tooth is worn mesiobuccally, preventing any determination of the configuration of the metastyle.

List of Selected Characters for the Cladistic Analyses

Dental, cranial, and postcranial characters and character states used in the phylogenetic analysis. Characters followed by an asterisk are considered "ordered". Some characters have been modified (different character state interpretation) from the original works (see Character references). These characters have been labeled by " ' " or " " ". A score of " ? " is used if information is unavailable due to a lack of material or if the character does not apply to a particular taxon. Tooth areas are calculated as the product of mesiodistal (md) length and buccolingual (bl) breadth.

Lower Teeth.

Incisors.

I1*. Lower incisor number: 0 = three; 1 = two; 2 = one: I_1 present, I_2 absent; 3 = lower incisors absent.

I2. Lower incisor occlusal arrangement: 0 = arcuate battery from lateral perspective (U-shaped arcade); 1 = cusp tips staggered (V-shaped arcade).

I3. Lower incisor crown spacing: 0 = no spaces; 1 = spaces present between crowns.

I4. I_2-C diastema: 0 = present; 1 = absent.

I5*. I_{1-2} size (ratio of I_{1-2} area to M_1 area): 0 = very small (= 0.69); 1 = moderate sized (= 0.70, = 1.07); 2 = large (> 1.07).

I6*. I_1:I_2 proportions (ratio of I_1 area to I_2 area): 0 = I_1 much smaller than I_2 (< 0.65); 1 = I_1 smaller than I_2 (= 0.65, < 0.82); 2 = I_1 almost as large as I_2 (= 0.83, < 1.00); 3 = $I_1 > I_2$ (= 1.01, < 1.25); 4 = $I_1 >> I_2$ (= 1.25).

I7*. I_1 crown width (spatulate incisors only): 0 = considerably wider (m-d) than root (spatulate): 1 = narrow at apex, wider than root; 2 = "styliform" (crown apex approximately the same width as the cervical margin).

I8. I_2 crown cross-sectional shape (ratio of m-d length to b-l breadth): 0 = rounded oval (= 0.64); 1 = mesiodistally compressed (< 0.64).

I9*. Lower incisors crown height (crown heights judged from cementoenamel junction to crown tip on the buccal surface): 0 = low crowned; 1 = moderately high crowned; 2 = high crowned.

I10. I_{1-2} crown buccal outline: 0 = gently curved in lateral perspective; 1 = acutely curved.

I11*. Lower incisor roots: 0 = erect or vertical; 1 = slightly procumbent; 2 = very procumbent.

I12*. Lower incisor crowns: 0 = erect or vertical; 1 = procumbent; 2 = very procumbent.

I13. Tooth comb: 0 = absent; 1 = with three teeth; 2 = with two teeth.

I14. I_1 crown shape: 0 = spatulate; 1 = lanceolate, pointed.

I15. I_2 heel development (a lingual swelling at the base of crown): 0 = heel absent; 1 = heel present.

I16. Incisor lingual enamel: 0 = well developed; 1 = very thin or absent.

I17*. Lower first incisor lingual cingulum: 0 = absent to weak; 1 = strong but incomplete; 2 = strong and complete.

I19*. Relative size of I_1 to M_1 (based on occlusal areas): 0 = I_1 very small ($I_1 << M_1$); 1 = moderately enlarged ($I_1 <$ or $= M_1$); 2 = grossly enlarged ($I_1 > M_1$).

Canines.

C1*. Female C_1 cross-sectional area relative to molar cross sectional area: 0 = very small ($C_1/M_1 < 0.40$); 1 = moderate (= 0.4, < 0.80); 2 = large (= 0.80, = 1.20); very large (= 1.20)

c2*. $C^1/_1$ dimorphism (square root of male C_1 area/square root of female C_1 area): 0 = low (< 1.07); 1 = moderate (= 1.07, < 1.17); 2 = high (= 1.17).

c3. C_1 cross-sectional shape: 0 = rounded oval; 1 = mesiodistally compressed; 2 = buccolingually compressed.

C4. C_1 lingual crest development: 0 = rounded; 1 = sharp.

C5. Canine paracristid (not scored if species has canine incorporated into a tooth comb): 0 = oblique to occlusal plane; 1 = nearly horizontal to occlusal plane; 2 = forms part of cropping mechanism with $I_{1-2.}$

C6. Canine height (females): 0 = low, squat; 1 = narrow, short; 2 = tall, at or above tooth row.

Premolars.

P1. $P^1/_1$: 0 = present; 1 = absent

p2. P_2: 0 = present; 1 = absent.

P3. P_2 roots: 0 = single; 1 = double.

P4'. P_3 roots: 0 = single; 1 = double.

P4”. P_4 roots: 0 = single; 1 = double.

P5*. Premolar crowding (overlapping of crowns): 0 = no crowding; 1 = slightly crowded; 2 = very crowded—mesial root positioned buccal to distal root.

P6*. P_3 paraconid: 0 = large; 1 = small; 2 = absent or extremely small.

P7*. P_4 paraconid: 0 = large; 1 = small; 2 = absent or extremely small.

P9’*. P_4 paraconid position (labiolingually): 0 = mesial to protoconid; 1 = mesiolingual, between protoconid and metaconid; 2 = mesial to metaconid.

P9’’. P4 paraconid position (mesiodistally): 0 = widely spaced from the metaconid ; 1 = twinned with metaconid.

P11*. P_{3-4} cristid obliqua: 0 = absent; 1 = weak; 2 = strong.

P13. P_2 protoconid height and shape: 0 = slender, projects above protoconids of P_{3-4}; 1 = massive, projects above protoconids of P_{3-4}; 2 = not projecting, in line with P_3; 3 = extremely short, shorter than P_3.

P14. P_4 metaconid position: 0 = close to protoconid; 1 = widely spaced from protoconid.

P15. P_2 metaconid size: 0 = absent or trace; 1 = small.

P16*. P_3 metaconid size: 0 = absent or trace; 1 = small; 2 = large (as big as protoconid).

P17*. P_4 metaconid size: 0 = absent or trace; 1 = small; 2 = large (as big as protoconid).

P18. P_4 trigonid—configuration of lingual wall : 0 = closed; 1 = open.

P19. P_3 entoconid and lingual talonid crest: 0 = absent; 1 = lingual talonid crest present but an entoconid does not stand out above it; 2 = entoconid forms a small discrete cusp.

P20. P_4 entoconid and lingual talonid crest: 0 = absent; 1 = lingual talonid crest present but an entoconid does not stand out above it; 2 = entoconid forms a small discrete cusp.

P21. P_4 lateral and medial protocristid: 0 = continuous between metaconid and protoconid; 1 = discontinuous between metaconid and protoconid.

P22. P_3 lateral protocristid orientation: 0 = transversely oriented; 1 = distolingually oriented; 2 = absent.

P23. P_4 lateral protocristid orientation: 0 = transversely oriented; 1 = distolingually oriented.

P24. P_{3-4} posterior trigonid wall: 0 = complete [taxa without metaconids are assigned this character state]; 1 = deeply notched.

P25. P_{3-4} hypoconid size: 0 = large; 1 = small or absent.

P26. P_{3-4} hypoconid (or distal terminus of oblique cristid) position: 0 = distal to protoconid; 1 = distal to metaconid, or between protoconid and metaconid

p27*. P_4 hypocristid shearing development: 0 = absent; 1 = weak; 2 = strong.

P28*. P_2 buccal cingulum development: 0 = absent; 1 = incomplete, broken at protoconid and hypoconid; 2 = complete.

P29*. Lower premolar inflation: 0 = not basally inflated; 1 = slightly basally inflated; 2 = very basally inflated.

P30*. P_4 exodaenodonty: 0 = not exodaenodont; 1 = slightly exodaenodont; 2 = very exodaenodont.

P31*. P_4 talonid length (ratio of midline m-d length of trigonid to m-d length of talonid): 0 = extremely short or non-existent (tri:tal = 1.61); 1 = short (much shorter than trigonid) (tri:tal = 1.27, < 1.61); 2 = equal or slightly shorter in length to trigonid (tri:tal = 0.92, < 1.27); 3 = talonid longer than trigonid (tri:tal < 0.91).

p33*. Premolar orientation: 0 = Crown bases vertical in lateral perspective; 1 = slightly oblique; 2 = strongly oblique, projecting medial over the anterior.

P34. P_4 anterobuccal cingulum development: 0 = absent or trace; 1 = strong.

P36*. P_4 postprotoconid ridge: 0 = weak or absent; 1 = moderate; 2 = very strong.

P37*. P_4 postmetaconid ridge: 0 = weak or absent; 1 = moderate; 2 = very strong.

P40*. P_4 paraconid height: 0 = low; 1 = moderate; 2 = high (nearly as high as protoconid).

P41*. P_{3-4} protoconid height: 0 = P_3 much lower than P_4; 1 = P_3 slightly lower than P_4; 2 = P_3 equal in height to P_4; 3 = P_3 higher than P_4.

P42*. P_3 to P_4 area: 0 = 0.45-0.59; 1 = 0.60-0.69; 2 = 0.70-0.79; 3 = 0.80.

p43*. P_4 m-d L/ b-l W: 0 = (< 0.95); 1 = (= 0.96, < 1.14); 2 = (= 1.15, < 1.20); 3 = (= 1.21, < 1.35; 4 = (= 1.36, < 1.46); 5 = (> 1.47).

p44*. Ratio of P_4 area to M_1 area: 0 = (< 0.62); 1 = (= 0.63, < 0.72); 2 = (= 0.73, < 0.82); 3 = (= 0.83, < 0.92); 4 = (= 0.93, < 1.02); 5 = (> 1.03).

p45. P_{3-4} root orientation: 0 = P_{3-4} roots aligned mesiodistally; 1 = P_3 root shifted laterally, P_4 mesial root aligned mesiodistally; 2 = P_3 roots aligned mesiodistally, P_4 mesial root shifted laterally. [Scored as missing if roots are single].

Molars.

M1. M_3: 0 = present; 1 = absent.

M2. M_1 root number: 0 = one; 1 = two.

M3. M_2 root number: 0 = one; 1 = two.

M4. M_3 root number: 0 = one; 1 = two.

M6*. M_2 trigonid width (ratio of buccolingual breadths of trigonid and talonid): 0 = much wider than talonid (= 1.11); 1 = widths similar (< 1.11, > 0.90); 2 = much narrower than talonid (= 0.90).

m7*. M_3 trigonid width (based on relative buccolingual breadths): 0 = much wider than talonid (= 1.20); 1 = trigonid and talonid widths similar (= 1.20-1.05); 2 = trigonid narrower than talonid (< 1.05).

m8'*. M_1 paraconid position: 0 = mesial to protoconid; 1 = mesiolingual, between protoconid and metaconid; 2 = mesial to metaconid.

M9'*. M_2 paraconid position: 0 = mesial to protoconid; 1 = mesiolingual, between protoconid and metaconid; 2 = mesial to metaconid.

M10*. M_3 paraconid position: 0 = mesial to protoconid; 1 = mesiolingual, between protoconid and metaconid; 2 = mesial to metaconid.

M8-9-10'. M_{2-3} paraconid location: 0 = widely spaced from the metaconid; 1 = twinned with metaconid.

M11. M_1 parastylid: 0 = absent; 1 = present.

M12*. Molar metastylids (postmetacristids): 0 = absent; 1 = small; 2 = large.

M13. M_3 hypoconulid: 0 = single; 1 = double

m14*. M_3 heel: 0 = absent; 1 = narrower than talonid; 2 = approximately equal in width to talonid.

M15*. Molar enamel surface: 0 = smooth; 1 = slightly crenulated; 2 = highly crenulated.

M16*. M_1 trigonid height (ratio of trigonid height to talonid height measured on the buccal aspect of the crown): 0 = higher than talonid (= 1.20); 1 = slightly higher than talonid (= 1.10, < 1.20); 2 = trigonid and talonid of similar height(< 1.10).

m17. M_{1-2} cusp relief: 0 = moderate to high; 1 = low.

M18. M_1 trigonid lingual configuration: 0 = open; 1 = closed.

M19. M_1 metaconid position: 0 = transversely aligned—lingual to protoconid; 1 = slightly distolingual to protoconid.

M20*. M_{1-2} paraconid development: 0 = absent; 1 = small; 2 = large.

M21. M_{1-2} lateral protocristid orientation: 0 = runs toward metaconid; 1 = runs toward hypoflexid.

M22. M_1 distal trigonid wall: 0 = complete; 1 = deeply notched by protoconid/metaconid sulcus; 2 = medial and lateral protocristid do not meet but no sulcus is visible.

M23. M_2 distal trigonid wall: 0 = complete; 1 = deeply notched by protoconid/ metaconid sulcus; 2 = medial and lateral protocristid do not meet but no sulcus is visible.

M24. M_{1-3} wear facet X: 0 = present; 1 = absent.

M25*. M_{1-2} entoconid: 0 = absent; 1 = barely stands out on lingual talonid marginal crest; 2 = a small discrete cusp; 3 = a large cusp.

M26*. M_{1-2} postentoconid sulcus: 0 = prominent; 1 = faintly visible; 2 = absent.

M27*. M_1 hypoconulid size: 0 = large; 1 = moderate; 2 = small; 3 = absent.

M28*. M_2 hypoconulid size: 0 = large; 1 = moderate; 2 = small; 3 = absent.

M29*. M_3 hypoconulid size: 0 = large; 1 = moderate; 2 = small; 3 = absent.

M30*. M_{1-2} hypoconulid position: 0 = twinned to entoconid; 1 = near midline; 2 = slightly buccal to midline.

M31*. M_{1-2} cristid obliqua development: 0 = weak (rounded); 1 = strong (trenchant); 2 = very strong (trenchant).

M32*. M_1 cristid obliqua orientation: 0 = reaches trigonid wall at a point distal to protoconid; 1 = reaches trigonid wall at a point distolingual to protoconid; 2 = reaches trigonid wall at a point distal to metaconid.

M33*. M_2 cristid obliqua orientation: 0 = reaches trigonid wall at a point distal to protoconid; 1 = reaches trigonid wall at a point distolingual to protoconid; 2 = reaches trigonid wall at a point distal to metaconid.

M34. M_1 cristid obliqua terminus: 0 = runs to base of trigonid; 1 = runs part way up the distal trigonid wall; 2 = connects with protoconid tip or protocristid; 3 = connects with metaconid.

M35. M_2 cristid obliqua terminus: 0 = runs to base of trigonid; 1 = runs part way up the distal trigonid wall; 2 = connects with protoconid tip or protocristid; 3 = connects with metaconid.

M36. M_3 cristid obliqua terminus: 0 = runs to base of trigonid; 1 = runs part way up the distal trigonid wall; 2 = connects with protoconid tip or protocristid; 3 = connects with metaconid.

M37. M_{1-2} centroconid development: 0 = present; 1 = absent but cristid obliqua bends sharply in hypoflexid; 2 = absent.

M38*. M_{1-2} hypocristid development: 0 = absent or seen only as a trace; 1 = weak; 2 = strong.

M39*. M_3 hypocristid development: 0 = absent or seen only as a trace; 1 = weak; 2 = strong.

M40*. Lingual configuration of M_{1-2} talonid: 0 = open; 1 = notched lingually but not open; 2 = closed.

M41. M_{1-2} distal fovea: 0 = absent; 1 = present (weak); 2 = present (large).

M42. M_{1-2} hypocristid configuration: 0 = simple; 1 = with accessory cusp close to hypoconid.

M43. M_{1-2} cristid obliqua: 0 = notched; 1 = straight.

M44*. Molar cusp inflation: 0 = cusps not inflated, marginally positioned; 1 = slightly inflated; 2 = very inflated.

M45*. M_{1-2} buccal cingulum development: 0 = absent to trace; 1 = partial, broken at protoconid and hypoconid; 2 = complete.

M46*. M_1 hypoflexid depth: 0 = very shallow; 1 = moderate; 2 = deep.

M47*. M_2 hypoflexid depth: 0 = very shallow; 1 = moderate; 2 = deep.

M53*. Ratio of M_2 length to M_3 length: 0 = M_3 much longer than M_2 (0.71-0.80); 1 = M_3 longer than M_2 (0.81-0.90); 2 = M_3 equal than M_2 (0.91-1.00); 3 = M_3 smaller than M_2 (1.01-1.12); 4 = M_3 much smaller than M_2 (= 1.13); 5 = if M_3 absent.

M55*. M_1 mesiodistal length/buccolingual breadth: 0 = 1.0-1.15; 1 = 1.16-1.22; 2 = 1.23-1.32; 3 = > 1.33.

m56. Convergence of buccal and lingual molar cusp walls: 0 = convergent; 1 = vertically sided.

M57. M_{1-2} entoconid position relative to hypoconid: 0 = transverse to hypoconid; 1 = distal to hypoconid.

ML88*. M_{1-3} Pre-entocristid: 0 = indistinct to absent; 1 = weakly developed (low); 2 = well-developed (strong and high).

Upper Teeth.

Incisors.

I1*. I^1-I^2 interstitial contact: 0 = absent; teeth widely spaced; 1 = present as narrow contact; 2 = I^2 tightly packed against I^1, I^1 preparacrista abbreviated.

I2. I^1-I^1 interstitial contact: 0 = present; 1 = absent: a wide space occurs in the midline between these teeth.

I3. I^2-C diastema: 0 = present; 1 = absent.

I4*. I^1 area:I^2 area: 0 = areas approximately equal (= 1.00); 1 = I^1 slightly larger than I^2 (> 1.00, < 1.40); 2 = I^1 much larger than I^2 (> 1.40).

I5*. I^1 size (I^1 area: M^1 area): 0 = incisor small (= 0.50); 1 = incisor moderate (> 0.50, < 0.56); 2 = incisor large (= 0.56).

I6*. I^1 occlusal shape (mesiodistal length/buccolingual breadth): 0 = rounded oval (< 1.05); 1 = buccolingually compressed (> 1.05, < 1.30); 2 = extremely compressed (> 1.30).

I7*. I^2 occlusal shape (mesiodistal length /buccolingual breadth): 0 = rounded oval (= 1.05); 1 = slightly buccolingually compressed (> 1.05, < 1.30); 2 = extremely buccolingually compressed = 1.30).

I8. I^1 crown shape: 0 = spatulate; no apparent occlusal cusp, mesial and distal edges continuous and rounded; 1 = semi-spatulate; central cusp present but blunt with discernable mesial and distal occlusal crests; 2 = central occlusal cusp pointed, occlusal edges steep.

I9. I^1 lingual fovea: 0 = simple; 1 = dual, with mid-crown pillar.

I10. I^1 occlusal edge orientation (for spatulate incisors only; all others scored as " ? "): 0 = occlusal edge orthogonal to long axis of root; 1 = occlusal edge wears at a steep angle to long axis of root; 2 = crown with pronounced mesial asymmetry (= mesial process) in unworn state.

I11*. I^{1-2} lingual cingulum: 0 = weak, discontinuous; 1 = moderate, continuous; 2 = strong.

I12. I^1 basal lingual cusp: 0 = absent; 1 = present.

I13. I^1-I^2 buccal cingulum: 0 = absent; 1 = present.

Canines.

C1. C^1 cross-sectional shape: 0 = oval; 1 = rounded.

C2*. Upper canine occlusion: 0 = C^1 wears against P_{1-2}; 1 = C^1 wears against P_2; 2 = C^1 wears against P_{2-3}; 3 = C^1 wears against P_3.

C3. C^1 mesial groove (females): 0 = shallow or absent; 1 = deep.

C4*. C^1 lingual cingulum: 0 = weak or absent; 1 = strong; 2 = very strong.

Premolars.

P1*. P^2 root number: 0 = one (if tooth is absent, taxon scored " 0 "); 1 = two; 2 = three.

P2*. P^3 root number: 0 = one; 1 = two; 2 = three.

P3*. P^4 root number: 0 = one; 1 = two; 2 = three.

P4*. Ratio of P^2 area to P^3 area: 0 = P^2 much smaller (= 0.85) (if tooth is absent, taxon scored " 0 "); 1 = P^2 smaller (> 0.85, < 0.95); 2 = P^2 equal (= 0.95).

P5*. Ratio of P^4 area to M^1 area: 0 = P^4 << M^1 (= 0.66); 1 = P^4 < M^1 (> 0.66, = 0.76); 2 = P^4 = M^1 (0.77-1.05); 3 = P^4 > M^1 (> 1.06).

P6. P^2 occlusal outline: 0 = triangular; 1 = suboval with the long axis b-l; 2 = suboval with the long axis m-d; 3 = round.

P7. P^4 occlusal outline: 0 = triangular; 1 = suboval; 2 = squared.

P8. P^{3-4} trigon/talon proportions: 0 = trigon > = talon; 1 = trigon < talon.

P9. P^3 protocone: 0 = present; 1 = absent.

P10. P^4 metacone: 0 = absent; 1 = present.

P11. P^4 protocone: 0 = low relative to paracone; 1 = high relative to paracone.

P12. P^2 protocone: 0 = present; 1 = absent (if tooth absent, taxon scored " 1 ").

P13'. P^2 hypocone: 0 = absent; 1 = present·

P14*. P^4 paraconule: 0 = large; 1 = small; 2 = absent.

P15. P^{3-4} parastyles: 0 = present; 1 = absent.

P16. P^{3-4} metastyles: 0 = absent; 1 = present.

P17. P^{3-4} postprotocrista: 0 =strong; 1 = weak, short.

P18. P^{2-3} distal crown margin: 0 = smoothly rounded; 1 = waisted between buccal and lingual cusps.

P19. P^{3-4} lingual cingulum: 0 = absent or weak; 1 = strong.

P20. P^3 metacone: 0 = absent; 1 = present

P21. P^{3-4} buccal cingulum development: 0 = absent or weak; 1 = strong.

ML126*. P^4 hypocone: 0 = minute to absent; 1 = present but small; 2 = strong.

ML127*. P^3 hypocone: 0 = minute to absent; 1 = present but small; 2 = strong.

Molars.

M1*. M^{1-2} root number: 0 = three, three; 1 = three, two; 2 = two, two.

M2*. M^{3} root number: 0 = three; 1 = two; 2 = one.

M3*. M^{2} shape (bl/md): 0 = very transverse (> 1.65); 1 = transverse (< 1.65, > 1.30); 2 = squared (= 1.30).

M4*. Ratio of M^{1} area to M^{2} area: 0 = M^{1} >> M^{2} (= 1.40); 1 = M^{1} > M^{2} (< 1.40, > 1.0); 2 = M^{1} = M^{2} (= 1.0).

M7'*. M^{1-2} metaconule: 0 = absent; 1 = single; 2 = double.

M9*. M^{1-2} preprotoconule: 0 = absent; 1 = weak; 2 = strong.

M10*. M^{1} hypocone size: 0 = large; 1 = small; 2 = minute to absent.

M11*. M^{2} hypocone size: 0 = large; 1 = small; 2 = minute to absent.

M12'*. M^{1-2} hypocone position: 0 = distal, far lingual to protocone; 1 = distal, slightly lingual to protocone; 2 = distal, slightly buccal to protocone.

M13*. M^{1-2} prehypocrista development: 0 = absent; 1 = weak; 2 = strong, reaches to postprotocrista, encloses the talon lingually.

M14*. M^{3} prehypocrista development: 0 = absent; 1 = weak; 2 = strong, reaches to postprotocrista, encloses the talon lingually.

M15. M^{1} or M^{2} paraconule position: 0 = attached to preprotocrista; 1 = unattached to preprotocrista.

M16*. M^{1-2} metaconule: 0 = absent to indistinct; 1 = small; 2 = moderate; 3 = large.

M17'*. M^{1-2} mesostyle size: 0 = absent to indistinct; 1 = moderate; 2 = strong.

M17". M^{1-2} mesostyle position: 0 = attached to ectocrista; 1 = present on buccal cingulum.

M20*. P^{4}-M^{1} pericone: 0 = absent; 1 = small; 2 = large.

M22*. M^{1-3} lingual cingulum development: 0 = absent to indistinct; 1 = weak, broken; 2 = strong, complete.

M24*. M^{1-2} buccal cingulum development: 0 = absent to indistinct; 1 = weak; 2 = strong.

M27. M^{1-2} pre-metaconule cristae: 0 = absent or weak; 1 = strong

M28. M^{1-2} post-metaconule cristae: 0 = absent or weak; 1 = strong

M30*. M^{3} paraconule: 0 = absent; 1 = small-moderate; 2 = large

M31*. Molar protocone lingual inflation: 0 = not inflated; 1 = slightly inflated; 2 = very inflated.

M33*. M^2 buccal expansion of paracone (specify which tooth): 0 = no expansion; 1 = slight expansion; 2 = considerable expansion.

M34*. M^3 metacone: 0 = absent or very small; 1 = moderate (but smaller than paracone; 2 = large (equal to paracone).

M36*. M^3 hypocone: 0 = absent or very small; 1 = small; 2 = large.

M37*. M^1 paraconule size: 0 = absent; 1 = small-moderate (smaller than paracone); 2 = large (nearly as large as or larger than paracone).

M44*. M^{1-3} anterior cingulum: 0 = strong, complete, long (connected to parastyle); 1 = strong, short; 2 = weak or absent.

M46*. M^3 size relative to M^1: 0 = very small (half the size of M^1 or less); 1 = small (two thirds); 2 = large (approximately as large).

ML147*. M^{1-2} metastyle: 0 = indistinct to absent; 1 = moderate; 2 = strong.

ML148*. M^{1-2} parastyle: 0 = indistinct to absent; 1 = moderate; 2 = strong.

ML149. M^{1-2} parastyle position: 0 = mesial to paracone; 1 = mesiobuccal to paracone.

ML150. M^{1-2} metastyle position: 0 = distal to metacone; 1 = distobuccal to metacone.

ML151*. M^{1-3} posterior cingulum: 0 = weakly developed; 1 = moderate, does not reach the metastyle; 2 = connected to metastyle.

ML152*. M^{1-3} posterior margin (waisted between buccal and lingual cusps): 0 = indistinct to absent; 1 = present but shallow; 2 = present, deep.

ML153*. M^{1-2} postparacrista: 0 = indistinct to absent; 1 = weakly developed; 2 = well developed (but well-marked notch between postparacrista and premetacrista); 3 = strongly elevated (weak notch between postparacrista and premetacrista).

ML154*. M^{1-2} premetacrista: 0 = indistinct to absent; 1 = weakly developed; 2 = well developed (but well-marked notch between premetacrista and postparacrista); 3 = strongly elevated (weak notch between premetacrista and postparacrista).

ML155. M^{1-3} protocone arrangement: 0 = normal position; 1 = oblique.

ML156. M^{1-2} postprotocrista development: 0 = strong; 1 = tiny.

ML157*. M^1 postprotocrista length: 0 = indistinct to absent; 1 = short; 2 = long.

ML158*. M^2 postprotocrista length: 0 = indistinct to absent; 1 = short; 2 = long.

ML159. M^1 postprotocrista direction: 0 = transverse, directed toward metaconule (or virtual metaconule emplacement); 1 = lateral, directed toward the lingual posterior cingulum (post-protocone fold-like).

ML160. M^2 postprotocrista direction: 0 = transverse, directed toward metaconule (or virtual metaconule emplacement); 1 = lateral, directed toward lingual posterior cingulum (post-protocone fold-like).

ML161. M^1 postprotocrista terminus: 0 = runs to base of metacone (with hypometacrista); 1 = runs to metaconule (at the level of the small or virtual metaconule); 2 = runs to posterior cingulum; 3 = limited at a point distal to protocone.

ML162. M^2 postprotocrista terminus: 0 = runs to base of metacone (with hypometacrista); 1 = runs to metaconule (at the level of the small or virtual metaconule); 2 = runs to posterior cingulum; 3 = limited at a point distal to protocone.

ML163. M^{1-2} preprotocrista: 0 = low; 1 = elevated.

ML164. M^1 preprotocrista connection (buccal side): 0 = connected between paracone and parastyle (by way of preparaconule crista); 1 = connected to parastyle (by way of preparaconule crista); 2 = connected to paraconule (or near to it or to a virtual paraconule).

ML165. M^2 preprotocrista connection (buccal side): 0 = connected between paracone and parastyle (by way of preparaconule crista); 1 = connected to parastyle (by way of preparaconule crista); 2 = connected to paraconule (or near to it or to a virtual paraconule).

ML166*. M^{1-2} postparaconule crista: 0 = indistinct to absent; 1 = moderate; 2 = well-developed (connected to paracone).

ML168*. M^{1-2} hypometacrista: 0 = absent; 1 = weakly developed (low and short); 2 = well-developed (high).

ML169*. M^{1-2} hypoparacrista: 0 = absent; 1 = weakly developed (short); 2 = well-developed (high).

MLN*. Hypometaconulecrista: 0 = indistinct to absent; 1 = moderate (not connected to protocone); 2 = well-developed (connected to protocone or postprotocrista).

Cranial characters.

Cr 1. Transverse septum arising from the cochlear housing: 0 = Absent; 1 = present and forming the lateral wall of an anterior accessory cavity pneumatized from the tympanic cavity; 2 = present and forming the lateral wall of an anterior accessory cavity pneumatized from the epitympanic recess.

Cr 2. Extent of pneumatization of anterior accessory cavity: 0 = Anterior accessory cavity lies anterior to the tympanic cavity and is not trabeculated; 1 = anterior accessory cavity extends medial to the tympanic cavity, and is trabeculated.

Cr 3. Pneumatization of mastoid (from epitympanic recess?): 0 = absent; 1 = present.

Cr 4. Presence or absence of perbullar pathway: 0 = absent; 1 = present and formed exclusively by the petrosal bone.

Cr 5. Anteroposterior location of posterior carotid foramen in bulla: 0 = Posterior to line joining midpoints of tympanic bones; 1 = anterior to this line.

Cr 6*. Mediolateral position of posterior carotid foramen in bulla: 0 = medial; 1 = midline of the bulla; 2 = lateral.

Cr 7. Ventrodorsal position of the carotid foramen in the bulla: 0 = dorsal, adjacent to basioccipital or mastoid bone; 1 = ventral.

Cr 8*. Position of posterior carotid foramen relative to fenestra cochleae: 0 = posterior; 1 = ventral; 2 = anterior.

Cr 9. Position of the internal carotid canal relative to the fenestra cochleae: 0 = runs across ventral lip of the fenestra cochleae, shielding it from ventral view when a canal is present; 1 = internal carotid canal does not shield the fenestra cochleae from ventral view.

Cr 10. Position of the portion of the internal carotid/promontory artery (or its accompanying nerves) lying on the promontorium anterior to the fenestra cochleae: 0 = on ventrolateral surface of promontorium; 1 = contacting only the cupula of the cochlea.

Cr 11. Size of stapedial and promontory canals: 0 = both stapedial and promontory canals are large; 1 = stapedial slightly smaller than promontory; 2 = stapedial highly reduced or absent altogether; 3 = stapedial larger than promontory; 4 = both promontory and stapedial canals absent.

Cr 12. Morphology of promontory canal, when present: 0 = open trough; 1 = complete canal.

Cr 13. Presence or absence of canal for internal carotid artery or nerves: 0 = absent; 1 = present.

Cr 14. Position of ventral edge of the tympanic bone: 0 = intrabullar, or aphaneric; 1 = extrabullar or phaneric.

Cr 15. The shape of the tympanic bone: 0 = ribbon-like or only slightly expanded; 1 = laterally expanded into a collar or tube; ? = due to fusion with surrounding bones, of unknown shape.

Cr 16. Morphology of annular bridge: ? = This character is not analyzable in those taxa with an extrabullar tympanic, or those in which this region is not known; 0 = Linea semicircularis or partial anular bridge formed on a entotympanic bulla; 1 = linea semicircularis formed on a petrosal bulla; 2 = a complete annular bridge.

Cr 17. Encroachment of the auditory bulla on the pterygoid fossa: 0 = absent; 1 = present and formed by anterior accessory cavity; 2 = present and formed by the tympanic cavity.

Cr 18. Nature of contact between the lateral pterygoid plate and the bulla wall: 0 = absent; 1 = laminar; 2 = abutting.

Cr 19. Extent of contact between the lateral pterygoid plate and the bulla wall: 0 = slight; 1 = or very extensive.

Cr 20. Flange of basioccipital overlapping medial bulla wall: 0 = absent or minimal; 1 = extensive.

Cr 21. Suprameatal foramen: 0 = absent; 1 = present, small and in the posterior root of the zygomatic arch; 2 = present, large, and above the external auditory meatus.

Cr 22. Patent parotic fissure: 0 = present; 1 = absent.

Cr 23*. Size of orbits: 0 = small; 1 = large; 2 = extremely large.

Cr 24*. Postorbital closure: 0 = none; 1 = postorbital bar present; 2 = postorbital septum present.

Cr 25. Composition of the postorbital septum: 0 = zygomatic forms most of the septum; 1 = frontal forms most of the septum.

Cr 26. Zygomatic-lacrimal contact: 0 = present; 1 = absent.

Cr 27. Pronounced interorbital constriction: 0 = absent; 1 = present below olfactory tract.

Cr 28. Contact between lacrimal and palatine: 0 = present; 1 = separated by a large fronto-maxillary contact (and in some taxa, a small os planum of the ethmoid); 2 = separated by a large os planum.

Cr 29. Foramen rotundum: 0 = absent; 1 = present.

Cr 30. Position of lacrimal foramen: 0 = outside orbital margin; 1 = within the orbit or on the rim.

Cr 31. Metopic suture in adult: 0 = unfused; 1 = fused.

Cr 32. Orbital convergence: 0 = less convergent than primates; 1 = primate-like values for convergence.

Cr 33*. Posterior nasal spine: 0 = reduced or absent; 1 = small but distinct; 2 = robust and long

Cr 34. Posterior palatine torus: 0 = present; 1 = absent.

Cr 35. Pyramidal processes: 0 = medially placed; 1 = laterally placed.

Cr 36*. Length of medial pterygoid plate: 0 = long medial pterygoid plate extending one-third to one half of the distance to the anterior surface of the bulla; 1 = short but distinct from lateral pterygoid plate for its entire dorsoventral extent; 2 = medial pterygoid plate entirely absent, or reduced to a low rugosity.

Cr 37. Snout length: 0 = long snouts; 1 = short snouts.

Cr 38. Maxillary depth: 0 = deep; 1 = shallow.

Cr 39. Complete symphyseal fusion: 0 = absent; 1 = present.

Cr 40. Temporomandibular joint morphology: 0 = biconcave and transversely wide; 1 = anteroposteriorly oriented trough.

Cr 41. Entoglenoid process morphology: 0 = weak or absent; 1 = strong.

Cr 42. Inter-incisor diastema width: 0 = broad and wider than that of extant haplorhines; 1 = narrow, haplorhine-like.

Cr43. Coronoid height relative to condyle: 0 = very far above; 1 = slightly above or equal.

Cr44*. Condyle height relative to toothrow: 0 = at level of tooth row; 1 = slightly above; 2 = well above tooth row.

Cr45. Corpus robusticity: 0 = shallow; 1 = deep.

Cr46. Zygomatico-parietal contact at pterion: 0 = no postorbital closure; 1 = zygomatico-parietal contact; 2 = alisphenoid-frontal contact.

Cr47. Enclosure of intratympanic portion of facial nerve in a bony canal: 0 = no canal, facial runs in a sulcus; = bony canal present.

Cr48. Epitympanic crest: 0 = absent; 1 = present.

Cr49. Broad ascending wing of premaxilla: 0 = narrow; 1 = broad.

Cr 50/301. Basioccipital stem: 0 = narrow; 1 = broad.

Cr51/302. Choanal shape: 0 = narrow; 1 = broad.

Cr52/292. Orientation of the mandibular symphysis: 0 = symphysis procumbent; 1 = symphysis erect.

Postcranial characters.

Humerus.

H1*. Shape of distal edge of the humeral trochlea: 0 = cylinder, distal edge perpendicular to shaft; 1 = distal edge somewhat angled to shaft; 2 = distal edge very angled.

H2. Relative heights of medial and lateral edges of humeral trochlea: 0 = subequal; 1 = medial edge more flared than lateral edge.

H3*. Trochleocapitular ridge: 0 = absent; 1 = weak but distinct; 2 = moderately distinct; 3 = very distinct.

H4. Waisted trochlea (Minimum trochlear diameter/maximum trochlear diameter x 100): 0 = > 70 (unwaisted); 1 = $\leq$ 70 (waisted).

H5*. Width of capitulum relative to trochlea (100 x ventral capitulum width/ventral trochlear width): 0 = < 100; 1 = between 100 and 140; 2 = 140-200; 3 = greater than 200.

H6. Entepicondylar foramen: 0 = present; 1 = variable; 2 = absent .

H7. Entepicondylar foramen position: 0 = above medial epicondyle; 1 = above ventral trochlea; 2 = above dorsal trochlea.

H8. Medial epicondyle size: 0 = reduced; 1 = prominent.

H9. Dorsal placement of medial epicondyle: 0 = parallel ; 1 = slight dorsal; 2 = large dorsal angle.

H10'*. Shape of the lateral edge of the dorsal trochlea: 0 = not pronounced; 1 = moderately pronounced; 2 = very pronounced.

H10"*. Shape of the medial edge of the dorsal trochlea: 0 = not pronounced; 1 = moderately pronounced; 2 = very pronounced.

H11*. Dorsoepitrochlear fossa: 0 = present (strong); 1 = small, shallow; 2 = absent.

H12*. Olecranon fossa shape: 0 = shallow; 1 = moderate; 2 = deep.

H13. Supinator crest: 0 = prominent; 1 = low.

H14*. Brachialis flange; 0 = broad; 1 = moderate; 2 = narrow.

H15. Bicipital groove morphology: 0 = shallow; 1 = deep.

H16. Deltopectoral crest: 0 = prominent; 1 = low; 2 = flattened superiorly.

H17. Deltotriceps crest: 0 = low; 1 = prominent.

H18/. Capitular tail: 0 = ventral articular wdth <2.5 times the ventral capitular width; 1 = ventral articular wdth > 2.5 times the ventral capitular width.

H19/*. Ratio of humerus length to femur length (H/F): 0 = 100* H/F = 65; 1 = H/F > 65, = 80; 2 = H/F > 80.

Carpal bones.

W1. Size of os centrale, orientation of centrale-trapezoid facet, and articulation with hamate: 0 = small os centrale, facet faces distally, no articulation with hamate; 1 = large centrale, facet faces distoradially, articulation with hamate.

W2. Ulnar-pisiform articulation: 0 = Facet on pisiform for ulnar styloid process is roughly equal in size to that for triquetrum; 1 = Facet on pisiform for ulnar styloid process is much enlarged and deeply excavated.

Os pelvis.

OP1/299. Gluteal tuberosity: 0 = present; 1 = absent.

OP2/300. Position of posterior gluteal tuberosity: 0 = Proximal to or level with lesser trochanter; 1 = distal to lesser trochanter.

Femur.

F1*. Length of femoral neck: 0 = $\leq$ 75; 1 = 75-120; 2 = $\geq$ 120.

F2*. Angle of femoral neck: 0 = < 60; 1 = 60-70; 2 = > 70.

F3. Angle of lesser trochanter: 0 = medial (0-30^{o}); 1 = posterior (>30^{o})

F4*. Size of third trochanter: 0 = large; 1 = small; 2 = low crest or absent.

F5*. Knee index (Antero-posterior diameter of distal femur/ mediolateral diameter of distal femur): 0 = < 90 (shallow knee); 1 = 90 – 100; 2 = > 100 (deep knee).

F6*. Femoral head shape: 0 = spherical; 1 = semicylindrical; 2 = cylindrical.

F7. Anterior extension of greater trochanter: 0 = no extension; 1 = extension present.

F8. Anterior bend of proximal femur: 0 = none; 1 = bent

F9*. Relative length of trochanteric fossa: 0 = long (> 125); 1 = moderate (110-125); 2 = very short (< 110).

F10. Presence of intertrochanteric crest: 0 = crest absent; 1 = crest present.

F11*. Size of lesser trochanter: 0 = large; 1 = intermediate; 2 = small.

F12. Lateral rim of knee: 0 = low; 1 = high.

Tibia.

T1'. Fusion of tibia and fibula: 0 = absent; 1 = present.

T1"*. Articulation tibia/fibula: 0 = small; 1 = moderate; 2 = extensive.

T3. Shape of distal surface of tibia: 0 = square/parallel; 1 = triangular.

T4*. Rotation of the medial malleolus: 0 = none; 1 = slight; 2 = strong.

T5*. Shape of medial malleolar articular surface: 0 = flat; 1 = anteriorly convex, posteriorly flat; 2 = all convex.

T6. Shape of distal tibial shaft: 0 = no compression; 1 = anteroposteriorly compressed.

T7. Position of tibialis posterior groove: 0 = on medial side of malleolus; 1 = on posterior side of malleolus.

Talus.

A1. Position of the flexor hallucis longus groove: 0 = lateral to trochlea; 1 = central to trochlea.

A2'*. Shape of talo-fibular facet: 0 = steep-sided; 1 = steep-sided with a platar lip; 2 = sloped obliquely.

A4'*. Development of the talar posterior trochlear shelf: 0 = none; 1 = weakly developed; 2 = well developed (prominent).

A5'. Talar neck length (NL/TL x 100): 0 = short (< 50); 1 = long (> 50).

A6. Medial talo-tibial facet: 0 = short (does not reach to plantar edge of bone); 1 = long.

A7/295. Lateral talar trochlear asymetry: 0 = absent; 1 = present.

A8/296. Talar cotylar fossa: 0 = shallow; 1 = deep, medially projecting.

A9'/297. Width of the head of the talus (HW/HHT x 100): 0 = < 120; 1 = > 120.

GEB1*. Talar neck angle: 0 = < 20°; 1 = 20-30°; 2 = > 30°.

GEB2*. Talar body height (HT/MTRW x 100): 0 = < 100; 1 = 100-120; 2 = 120-150.

GEB3*. TW/TL x 100: 0 = < 60; 1 = > 60.

Calcaneus.

C1*. Anterior calcaneal elongation: 0 = not elongate (ACL or anterior calcaneal ratio < 40); 1 = moderate (ACL = .40-45); 2 = long (> .45).

C2*. Position of the peroneal tubercle: 0 = distal to joint; 1 = at joint; 2 = proximal to joint.

C3. Posterior calcaneal bowing: 0 = absent; 1 = present.

C4/298. Calcaneo-cuboid articulation: 0 = articular wedge absent (fan-shaped); 1 = articular wedge present (more circular).

Navicular.

N1*. Length relative to width: 0 = short (<90); 1 = moderate (100-150); 2 = long (>150).

N3. Morphology of the naviculocuboid articulation: 0 = cuboid facet on navicular contacts only the ectocuneiform; 1 = cuboid facet contacts the ectocuneiform and mesocuneiform facet.

Entocuneiform.

E1*. Shape of Entocuneiform/MT1 articulation: 0 = dorsally reduced; 1 = dorsal moiety of joint enlarged relative to ventral moiety; 2 = dorsal moiety greatly enlarged.

E2. Lateral process of entocuneiform: 0 = small; 1 = hypertrophied.

General Foot.

O1. Foot axis: 0 = mesaxonic; 1 = paraxonic; 2 = ectaxonic.

O2. Toilet claw: 0 = absent; 1 = present.

O3. Prehallux: 0 = present; 1 = absent.

O4. Metatarsus length: 0 = short; 1 = long.

Metatarsal.

MT1*. Peroneal tubercle of MTI: 0 = very large; 1 = large; 2 = small.

MT2. Hallux length: 0 = short; 1 = long.

Visual system.

V1/288. Optic fovea: 0 = absent; 1 = present.

V2/290. Tapetum lucidum: 0 = present; 1 = absent.

Miscellaneous other characters.

289. Haplorhini vs strepsirrhine: 0 = strepsirrhine; 1 = haplorhine.

Molecular and physiological.

MOL1/303. SINE (short interspersed nuclear elements) markers at the human locations 12p13-pter on chromosome 12: 0 = SINE absent; 1 = SINE present.

MOL2/304. SINE (short interspersed nuclear elements) markers at the human location 7q22, on chromosome 7: 0 = SINE absent; 1 = SINE present.

MOL4/291. Ability to synthesize Vitamin C: 0 = synthysis possible; 1 = synthysis not possible.

Placentation.

PL1/305. Placentation: 0 = Diffuse, epitheliochorial; 1 = Discoidal, hemochorial.

PL2/306. Blastocyst attachment: 0 = noninvasive; 1 = invasive.

PL3/307. Amniotic cavity: 0 = primordial cavity absent; 1 = primordeal cavity present.

PL4/308. Choriovitteline placenta: 0 = present; 1 = absent.

PL5/309. Embryonic body stalk: 0 = absent; 1 = present.

PL6/310. Allantois development: 0 = large, vesicular; 1 = rudimentary.

Character sources:

- For details about the source of most characters (2-4);
- PL1/305, PL2/306, PL3/307, PL4/308, PL5/309, PL6/3010 (5,6);
- MOL1/303, MOL2/304, MOL3/305 (7, 8);
- MOL4/291 (9);
- 289 (10);
- V1/288, V2/290 (11);
- C4/298, A7/295, A8/296, A9/297, OP1/299, OP2/300, H18, H19, Cr50/301, Cr51/302 (12);
- Cr52/292 (13);
- A1, A2', A4, A5', A6, GEB1-3 (14);
- M8-9-10', ML88, ML126-127, ML147-169 (15).

Phylogenetic Analyses

The origin of Anthropoidea remains one of the most hotly contested issues in primate evolution. Furthermore, the nature of the phylogenetic relationships between Eocene Asian and Eocene-Oligocene African forms is still unclear and actively discussed. As a contribution to these phylogenetic debates, here we provide an assessment of the position and the role of these new primates from the Oligocene of Pakistan in a high-level phylogenetic context.

Material and methods

Selected Characters. We mainly used the updated compilation of characters (primarily morphological) and character states recently published by Kay *et al.* (4) on a large number of living and fossil primates, but substantially modified based on both personal observations and interpretations (see character list). Of the morphological characters, 207 are dental (3, 4, 15), 52 are cranial (3, 12, 13), 68 are postcranial (3, 6, 12), 3 are characters of the soft-tissues (4, 11), and 6 are developmental features (5, 16). Following Kay *et al.* (4), three molecular and physiological characters were included (7-9). All the selected characters are equally weighted. The multistate characters were considered as ordered (Option 1) if changes from one state to another required passing through intermediate states (17). With such an *ad hoc* assumption, character state assignments do not convey *a priori* judgments about character polarity (unconstrained parsimony). However, analyses were performed with unordered multistate characters as well (Option 2) in order to evaluate the effects of character ordering on tree topologies.

Selected Taxa. Our taxonomic sampling (see Table 2) derives from that of Ross *et al.* (3) and Kay *et al.* (4). However, some taxa were deleted (such as *Aycrossia*, *Ignacius*, *Pseudoloris*, *Rooneyia*, *Tetonoides*, and *Trogolemur*) because we did not have the opportunity to observe originals or casts of specimens for updating the dataset with respect to the changes we introduced on character descriptions and character states. On the other hand, several taxa were added to the dataset, those for which originals or casts were available in the collections of the University of Montpellier [UMC] (*Branisella*, *Guangxilemur*, *Hoanghonius*, *Moeripithecus*, *Neosaimiri*, *Oligopithecus*, *Periconodon*, *Phenacopithecus*, *Sivaladapis*, and *Xanthorhysis*).

As in previous studies (3, 4), some taxa included in the analysis were composites of several species of one genus (see Supporting Information: Matrix), or from unassociated specimens representing several areas of the body. The data set was systematically supplemented when possible. Within the Amphipithecidae, following Jaeger *et al.* (1), *Amphipithecus* may be considered as a junior synonym of *Pondaungia*. In this analysis, *Pondaungia* was, therefore, a composite of *Pondaungia* and "*Amphipithecus*" (small and large forms) for which morphological variations were included and pooled as polymorphism. Furthermore, cranial characters previously scored for *Amphipithecus* (characters CR23, 24, 31; see Character list) were not coded in this new matrix because the skull fragments attributed to this genus ("frontal bones") have been both incorrectly assigned and interpreted (18). As in the case of Ross *et al.* (3) and Kay *et al.* (4), Primates were examined within a context of higher-level phylogeny, together with Scandentia and Plesiadapiformes, which were designated as out-groups.

Phylogenetic Analyses. Data were managed by MACCLADE 3.04 (19). Phylogenetic reconstructions were performed by PAUP* 4.0 BETA 10 WIN (20). As the data set contained too many taxa for executing an exact search (Branch and Bound option), heuristic search methods (Hsearch) with a random step-wise addition (1,000 replications with randomized input order of taxa) and tree bisection-reconnection (TBR) branch-swapping options were applied.

Results and Comments

Heuristic searches performed on the data set including some ordered multistate characters (Option 1) have yielded two equally most-parsimonious trees of 2,810 steps each (CI = 0.273; RI = 0.53). Analyses made on the same data set but considering all characters unordered (Option 2) have yielded 38 trees of 2,646 steps each (CI = 0.289; RI = 0.51). In these latter analyses, most of the alternative topologies generated (equally parsimonious) mainly reflect the numerous irresolutions within the omomyid and adapid clades. Strict consensus trees of both types of analyses are presented in Fig. 6 *A* and *B*. Similar to the analyses of Kay *et al.* (4), we obtain in both cases (Option 1 and Option 2) the monophyly of the Amphipithecidae (nodes IV, Fig. 6 *A* and *B*) here including *Siamopithecus*, *Pondaungia*, *Myanmarpithecus* and *Bugtipithecus* – a result that supports the amphipithecid status of *Bugtipithecus*. Analyses performed with unordered multistate characters (Option 2) provide support for an eosimiid

clade including *Phileosimias* with *Eosimias*, *Phenacopithecus* and *Bahinia* (node II', Fig. 6*B*). By contrast, analyses considering some ordered multistate characters (Option 1) identify an eosimiid clade including *Eosimias*, *Phenacopithecus* and *Bahinia*, but to the exclusion of *Phileosimias* (node II, Fig. 6*A*). In this phylogenetic context, *Phileosimias* represents the most basal member of the larger anthropoid clade (node I', Fig. 6*A*), that is the sister group of Eosimiidae. Whatever the multistate character assumptions (ordered *versus* unordered), the results of these analyses consistently point toward the monophyly of a large clade (nodes I, Fig. 6 *A* and *B*) including Eosimiidae, Amphipithecidae, Oligopithecidae, Propliopithecidae, Proteopithecidae, Parapithecidae and platyrrhine primates. Assuming this clade to be the Anthropoidea clade, from the present evidence, eosimiids and amphipithecids (and by extension *Phileosimias* and *Bugtipithecus*, respectively) are stem anthropoids. The Eosimiidae represent the earliest offshoot of the Anthropoidea and the Amphipithecidae are the sister group of a smaller clade (nodes V, Fig. 6 *A* and *B*) consisting of Paleogene Arabo-African anthropoids (Parapithecidae, Proteopithecidae, Oligopithecidae, Propliopithecidae) and South American crown platyrrhines. Among the Afro-Arabian anthropoids, the Oligopithecidae (*Oligopithecus* and *Catopithecus*) are closely related to the Propliopithecidae (*Aegyptopithecus*, *Moeripithecus*) (nodes VI, Fig. 6 *A* and *B*), thus supporting the hypothesis that oligopithecids are crown anthropoids (3), more precisely stem catarrhines (12, 21), and not stem anthropoids as it had been previously argued (2, 3). Similar to the analyses of Kay *et al.* (4), our results reveal that *Proteopithecus* and *Serapia* (Proteopithecidae) are basal to Parapithecidae (here including *Apidium*, *Parapithecus*, *Simonsius*, *Qatrania*, and *Arsinoea*) (nodes IX, Fig. 6 *A* and *B*), thus suggesting that both taxa might be regarded as parapithecids (4, 22) and not stem platyrrhines (23, 24). Our phylogenetic scenario rather suggests that the "Proteopithecidae"-Parapithecidae clade is the stem group of crown platyrrhines (nodes VII, Fig. 6 *A* and *B*). However, the apparent sister group relationship between these Paleogene African primates and the neotropical crown platyrrhines does not preclude the existence (possibly out of Africa) of a more compelling candidate for the stem platyrrhine evolution. In all cases, our analyses do not support close relationship between platyrrhines and catarrhines (4, 18).

Concerning the phylogenetic position of the Anthropoidea in a higher-level primate phylogeny, the tarsiid-omomyid-anthropoid model of anthropoid origin receives greater support here than the adapiform-anthropoid or prosimian/anthropoid models. Only analyses performed with unordered multistate characters (Option 2) have generated, in addition to the

omomyid-tarsiid-anthropoid relationships, alternative topologies showing links between adapids-lemurs-lorises and tarsiids-anthropoids to the exclusion of omomyids, thus involving a trichotomy between the omomyid, tarsiid-anthropoid and adapiform clades on the strict consensus tree (Fig. 6*B*). The overall consensus emerging from both analyses primarily reflects the haplorhine (tarsiids, omomyids, anthropoids) / strepsirrhine (adapiforms, lemuriforms-lorisiforms) dichotomy, which is supported by a wide variety of neontological and paleontological data (2-4, 8, 11, 13, 16, 25-27). However, the two types of analyses performed (Option 1 and Option 2) offer substantially different phylogenetic scenarios regarding the tarsiid position (nodes X, Fig. 6 *A* and *B*) within the Haplorhini clade. The phylogenetic position of the Tarsiidae (here including *Tarsius*, *Xanthorhysis* and *Afrotarsius*) is perhaps the most controversial issue in primate phylogeny (ref. 28 for a review). Our results express in fact the two major and current variants of the Haplorhini concept. On the one hand, considering the Option 1 (Fig. 6*A*, node XI), Tarsiidae are nested within Omomyidae (which are paraphyletic; node XII, Fig. 6*A*) on the bases of characters from the cranial anatomy (13, 29). This scenario advocates a fundamental dichotomy within Haplorhini between Tarsiiformes (tarsiids + "omomyids"; node XII, Fig. 6*A*) and Anthropoidea (30-32), and therefore implies a long independent history for anthropoids. On the other hand, considering the Option 2 (Fig. 6*B*, node XI'), Tarsiidae and Anthropoidea are more closely related to each other than either is to omomyid primates (which are monophyletic; node XII', Fig. 6*B*). This scenario is based primarily on the presence of a postorbital septum in both modern tarsiers and anthropoids (+ Paleogene African forms), and on shared characters in the morphology of their auditory region (2-4, 33-35). However, there is ongoing debate as to whether these morphological characters, notably postorbital closure, are homologous between tarsiers and anthropoids (13, 36). Besides, there is no fossil evidence yet available for demonstrating that stem tarsiids (for instance *Xanthorhysis*) and stem anthropoids (eosimiids and amphipithecids) had already developed such a character. As suggested by Beard (32), "possibly, these highly diagnostic traits evolved relatively recently in anthropoid phylogeny", and in the tarsiid lineage as well. Whatever the higher-level pattern of relationships considered within the Haplorhini clade (i.e. "omomyids"-tarsiids to the exclusion of anthropoids *versus* tarsiids-anthropoids to the exclusion of omomyids), characters supporting a scenario become homoplasious when considering the other one. So, we do not attempt to resolve this phylogenetic issue since we do not provide here substantial fossil evidence, notably cranial evidence, for supporting one of these scenarios.

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